A NEW LABYRINTHODONT (*PARACYCLOTOSAURUS*) FROM THE UPPER TRIAS OF NEW SOUTH WALES

BY

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By D. M. S. WATSON

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I INTRODUCTION

THE Namurian rocks of New South Wales containing characteristic plants found also in Scotland, are succeeded by a great series of beds with a total thickness of 14,000 feet. The upper part—some 3,500 feet of this—forms the Hawkesbury Series, whose lowest element, the Narrabeen Beds, may perhaps be held to include the fish fauna from Gosford, described by Woodward (1890) and revised by Wade (1940). In the middle of the succeeding Hawkesbury Sandstone is the very rich fish fauna of Brookvale, described by Wade (1935), and that of the Wianamatta shales (which rest on the Hawkesbury Sandstone) of St. Peter's near Sydney, described by Woodward (1908) and revised by Wade (1941). The St. Peter's fish occur in shales, and the ironstone nodules in them, worked in a series of brick pits near Sydney. They were collected by Mr. B. Dunstan of the Geological Survey of New South Wales.

In one of these pits, about 1910, Mr. Dunstan found fragments of an enormous ironstone nodule which by most careful search he was able to reconstruct completely. The nodule contained a complete labyrinthodont skeleton which I saw in July 1914. It was immediately obvious that the animal was closely related to *Cyclotosaurus*, then known only by specimens from the lower part of the Upper Trias of Germany. This gave a well fixed correlation for at least one point in the Hawkesbury Series, the only one, indeed, in the whole succession of rocks set out above. It was therefore desirable that the position of " *Cyclotosaurus* " as a descendant of " *Capitosaurus* " should be established, and the time range through which it lived should be determined. This I undertook to do, and Sir Edgeworth David, after whom the species is named, arranged for the British Museum (Natural History) to acquire the specimen.

MATERIAL. The nodule (B.M.N.H. R.6000), some 9 feet (2·75 metres) long, is split roughly into dorsal and ventral halves, each composed of more than fifty blocks, some of which weigh nearly a hundredweight. The matrix is an extremely hard and brittle ironstone, quite impossible to work. As the bone was largely rotten, and much of it already lost, Mr. F. O. Barlow of the Museum staff removed all the remains of bone, even from the deepest fissures in the blocks. Many of the blocks are very heavy and irregular in shape, and it was impossible to place them together, run in a flexible casting medium, and so draw out complete casts of individual bones. In practice the cavities in a block and its counterpart had to be cast separately in glue. From the glue impression a waste mould was prepared from which, in turn, a plaster positive was made. This was then trimmed until it fitted accurately the cast of the same bone similarly prepared from the counterpart. The two parts were then fitted together and cast in a jelly mould which yielded perfect replicas that for all practical purposes are as good as the original bones. Details of the braincase, however, can only be determined by supplementing them with flexible plastic casts. Barlow's work covered many years, and I do not know of any other man who could have done it ; it was a technical triumph.

The articulated skeleton is complete, but the skull and lower jaws are distorted in a remarkable way. The mode of attachment of the head to the vertebral column is very difficult to determine, and some bones were broken and misplaced, evidently before burial. The fractures all lie in the same region, that of the hinder part of the head, lower jaws, and interclavicle. The skull, seen from above, is asymmetrical, the orbits evidently misplaced to the right. In direct dorsal view the lateral border of the right orbit lies 7 cm. from the margin of the skull at the front of the squamosal, the corresponding measurement on the left side being 11·5 cm. On the right side the outer surface is smoothly rounded from the mid-line at the parieto-dermosupra-occipital suture to the lower border of the quadratojugal. On the left the surface is concave and broken by a crack which has a displacement of a centimetre. This distortion extends forward to the anterior end, but scarcely affects the triangle of bone between the pineal foramen and the occipital border. On the palate the parasphenoid is broken at the ends of the sphenethmoid, the right pterygoid is crossed obliquely by a crack running backward from the hinder end of the right palatal vacuity, and the two occipital condyles are forced into contact. The left lower jaw seems to be undistorted, but the right is crushed down just in front of the opening through which the temporal muscles passed into it, so that its depth was decreased, its width increased, and the jaw as a whole bent upward and inward. These distortions agree with those of the palate. The interclavicle is crossed obliquely by a crack, matching those on the palate and skull roof, which posteriorly, on the left side, has a displacement of nearly one centimetre.

These breaks, and the displacements which result from them, lie almost entirely in the region behind the eyes, and can only reasonably be interpreted as the results of a single heavy blow, for it broke three horizontal sheets of bone—the skull roof, palate and interclavicle—each almost two centimetres thick. All these bones were surrounded and widely separated by soft tissues. Furthermore it appears from the results that such a blow must have been delivered by a massive cylindrical body, such as a tree trunk from the bank, falling across the animal ; the body afterwards being washed into the bottom of the lake.

II. SYSTEMATIC DESCRIPTION OF *PARACYCLOTOSAURUS DAVIDI* gen. et sp. nov.

Braincase. The braincase is almost completely underlain by the hinder part of the parasphenoid, which except for a short border between the exoccipitals, has continuous sutural attachments to them and to the pterygoids, the details being obscure. The ventral surface of the parasphenoid posteriorly bears a very low transverse ridge, behind which its surface is depressed, a condition associated with the attachment of recti capitis muscles. The greater part of its area is, however, shallowly concave, continuous with that of the pterygoid attached to it, whose surface turns down laterally. The whole directly supported the skin of the roof of the mouth. At the hinder margin of the palatal vacuity, where the pterygo-parasphenoid suture ends, the bone narrows, the narrowest point of the " processus cultriformis ", some 10 cm. in front, being only 19 mm. wide, with a cylindroid surface and a shallow groove—presumably occupied in life by a cartilaginous septum—on its upper surface. It then continues forward, widening and having a flat lower surface, until it is overlapped by the vomers, and ends by rising up above the junction of these bones.

Each exoccipital bears a large hemispheroidal condyle covered by cartilage during life to an extent shown by a projecting ridge, which marks the end of the dense bony sheet that coated its outer surface. Viewed as a pair it is evident that the condyles allowed dorso-ventral motion of the head, perhaps through a large arc, and inhibited any horizontal movement. The lateral surface of the condyle passes forward and outward to a suture with the pterygoid, forming a thick rounded flange, the floor of the tympanic cavity. Above the inner part of the condyle a thin flange passes horizontally inward above the space occupied by the persistently cartilaginous basioccipital. Its upper surface forms the floor of the brain cavity and laterally curves upwards and then slightly inwards to form the side walls of the brain cavity. A foramen in the lateral grove leads into a canal passing through the bone, which opens on the posterior surface of the exoccipital just above the condyle. It transmitted a XIIth nerve. Damage obscures the exit of the vagus. The upper part of the exoccipital is continuous with the descending process of the dermosupraoccipital and of the tabular. These are massive bones separated by a triangular post-temporal vacuity.

It is natural to suppose that, as in all earlier capitosaurs, there should be an abruptly truncated projecting process, mesial to the junction of the dermosupra-occipital and exoccipital, which supported a cartilaginous supraoccipital. On the

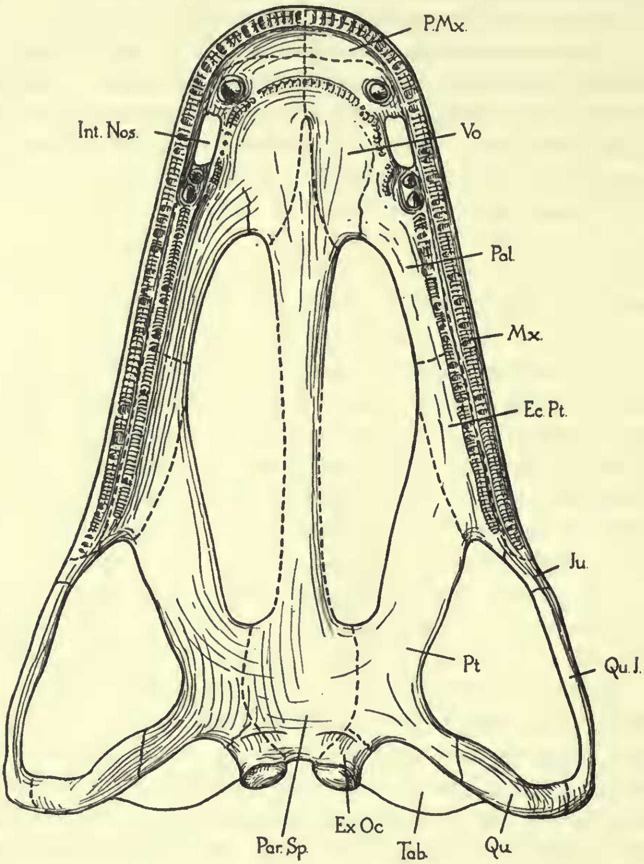

FIG. 1. *Paracyclotosaurus davidi* gen. et sp. nov. The palate. × 1/6. (For explanation of lettering see p. 263.)

left side the surface of the two bones is perfectly shown and there is no trace of the process, but the sculpturing seems to show that the surface abutted on to a supraoccipital cartilage. Dorsally there remains a space on the under surface of the dermosupraoccipitals, partially subdivided into three by low ridges, which was clearly open and perhaps occupied by blood vessels above a supraoccipital. This unusual arrangement seems to be well established here.

The position of the supraoccipital and paroccipital can only be inferred as there is no trace of ossification in them. A small shapeless ossification, high up in the proötic, is attached to the summit of the pre-tympanic flange of the left pterygoid. On its inner side, at the hinder edge, is a narrow groove forming a quadrant of a circle. Presumably it housed the anterior vertical semicircular canal.

Fortunately the stapes is in position on the right side, giving some indication of the relations between the proötic, paroccipital and exoccipital. The cartilaginous paroccipital must have been a small mass, meeting the proötic above the fenestra, lying in contact above with the exoccipital, and separated from it below by the vagus. Primitively the paroccipital reached the occipital process of the tabular. In the present specimen that process passes downward and inward as a thick sheet of bone, which meets and fuses with the corresponding process of the dermosupraoccipital and the exoccipital, the sutures being invisible.

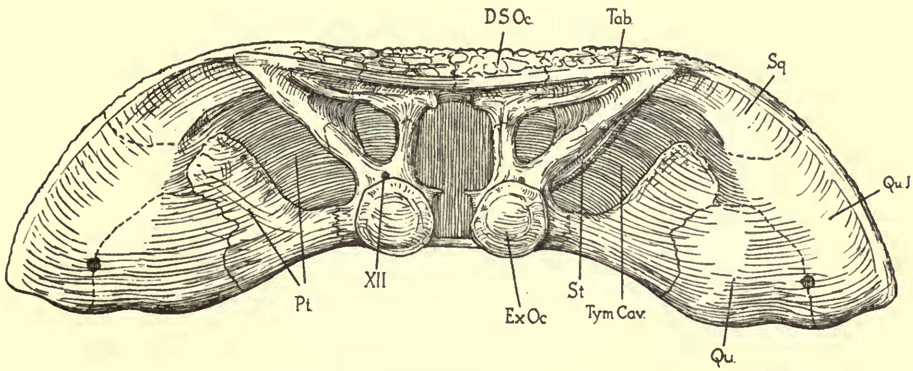

FIG. 2. *Paracyclotosaurus davidi*. The occiput. × 1/4.

The basisphenoid is entirely unossified. The impression of its lower surface on the parasphenoid, however, is easily interpreted by comparison with *Eryops*, and with a remarkable specimen of *Rhinesuchus* (B.118, D. M. S. W. Coll.). The key feature is the deep groove running transversely, housing a thickening of the lateral part of the basisphenoid, which extends into a pit excavated mainly in the mesial border of the pterygoid, and is roofed by the foot of the epipterygoid ; this is the basipterygoid process. The groove is supported behind by a deep flange which extends outward, increasing in depth as it does so, to end on the border of the fenestra ovalis, where the accessory process of the stapes is attached to it.

In front of the proötic the floor and side walls of the braincase are entirely unossified, but the epipterygoids which lie immediately lateral to it (and are in part modelled on the Gasserian ganglion) are well preserved. They are described later, with the quadrate and pterygoid.

The anterior part of the brain was set within a massive bony sphenethmoid. This is a single structure, lying in the grooved upper surface of the processus cultriformis of the parasphenoid, and reaching the dermal roof of the skull between, and in front of, the eyes. It has the following measurements : length about 11 cm., depth (including the parasphenoid) posteriorly 6·5 cm., and anteriorly 7·5 cm., maximum width at the upper edge 3·6 cm. posteriorly and 5·3 cm. anteriorly (all figures being approximations). The brain cavity within, measured on a natural cast, is posteriorly 2·6 cm. deep and 2·0 cm. wide. This cavity was divided into two independent canals (for olfactory lobes?) 7·0 cm. in front of the hinder end. There is no trace of any further ossification of the braincase, and no evidence about the olfactory capsules.

The ossifications in the palatoquadrate cartilage are well shown, and as they are attached to the braincase through the intermediary of the pterygoid, it is convenient to begin by describing this bone. The pterygoid is attached by a long suture to the lateral border of the parasphenoid and the front of the exoccipital. The attachment is by interlocking surfaces about 2·5 cm. thick, and about 15 cm. long. From the attachment the bone stretches outward, turning downward as it does so, the palate between the subtemporal fossae being concave and cylindrical. The palatal ramus

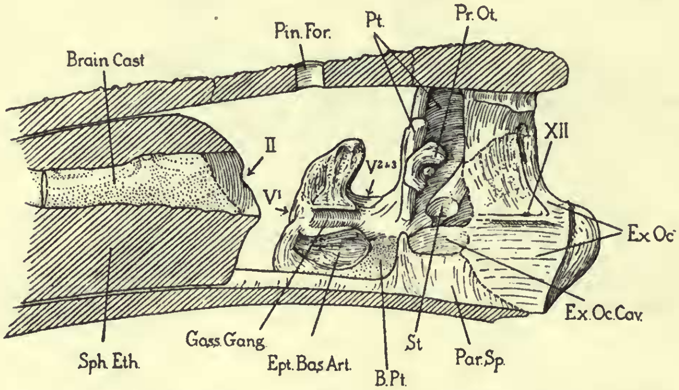

FIG. 3. *Paracyclotosaurus davidi.* Reconstruction of longitudinal section through the braincase along the middle line. × 1/3. The " brain " in the sphenethmoid is a drawing of a natural cast of the cavity.

turns forwards and outward to meet the narrow strip of palate lateral to the palatal vacuity, the suture being unseen. The quadrate ramus, which is well shown (Text-figs. 3, 4), is essentially a sheet of bone that rises abruptly from the flat lower part attached by suture to the parasphenoid. It has a rounded edge admesially, which rises immediately above the deep ridge on the parasphenoid limiting the basipterygoid process behind, to extend upward and end some distance below the skull roof. The proötic is attached to this edge. From this mesial border the paraotic flange of the pterygoid rising to the skull roof, passes outward swinging round a conical surface until it sweeps backward and outward to pass to the quadrate. There it ends, the two bones meeting in a thick abutment, rather than in a deep overlap. On its hinder surface (Text-fig. 2) the quadrate ramus of the pterygoid is divided into two areas ; the mesial (the anterior wall of the tympanic cavity) is a hollow cone, truncated below where the pterygoid and exoccipital meet, rising until it reaches the anterior border of the hole in the skull roof which housed the tympanic membrane. Laterally the pterygoid forms a triangular area that is attached to, but rises above, the quadrate. The summit of this area is sculptured for some other attachment, presumably that of a lateral wall of the tympanic chamber.

There are two ossifications in the palatoquadrate cartilage, which apparently persisted between them. The posterior, the quadrate, is a massive bone whose very wide lower surface is entirely occupied by the condyle for the articulation of the lower jaw. Above this the bone rises as a solid sheet (22 mm. thick above the thickened articular lower part) surrounded by the pterygoid, squamosal and quadratojugal, which together hold it in place. The attachment to the pterygoid is almost edge to

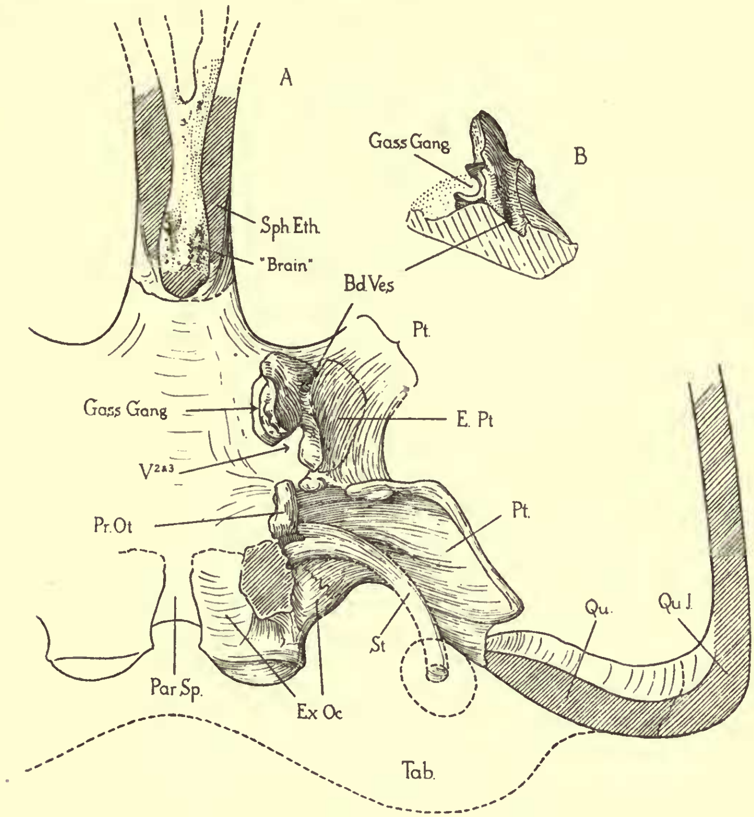

FIG. 4. *Paracyclotosaurus davidi*. A, the braincase and the parts in relation to it seen from above, with the dermal skull roof removed, and the right quadrate and quadratojugal cut at a lower level. B, the left epipterygoid viewed directly from in front. The drawing represents an actual glue cast from the original cavity. × 1/3.

edge, rather than the extensive overlap usual in labyrinthodonts. Ventrally, just above and mesial to the condylar surface, the quadrate ends in a narrow surface from which a cartilaginous strip 5 mm. thick extended forward, lying in a groove in the pterygoid, until it met an abrupt face on the hinder and lower border of the epipterygoid.

The epipterygoid is well ossified, and elaborate (Text-figs. 3, 4). Its base rests on the upper surface of the pterygoid, where that bone passes forward and outward behind the palatal vacuity, and was continued by cartilage back to the quadrate, and perhaps a little forward and outward. On the inner surface the bone has a projecting boss abruptly truncated where it was attached to the side of the cartilaginous basis cranii. Above this level the inner surface of the bone is crossed horizontally by a deep groove, bounded above and below by shallow but projecting flanges. In this the Gasserian ganglion lay, the ophthalmic branch of that nerve passing outward and forward in front, and the maxillary and mandibular branches

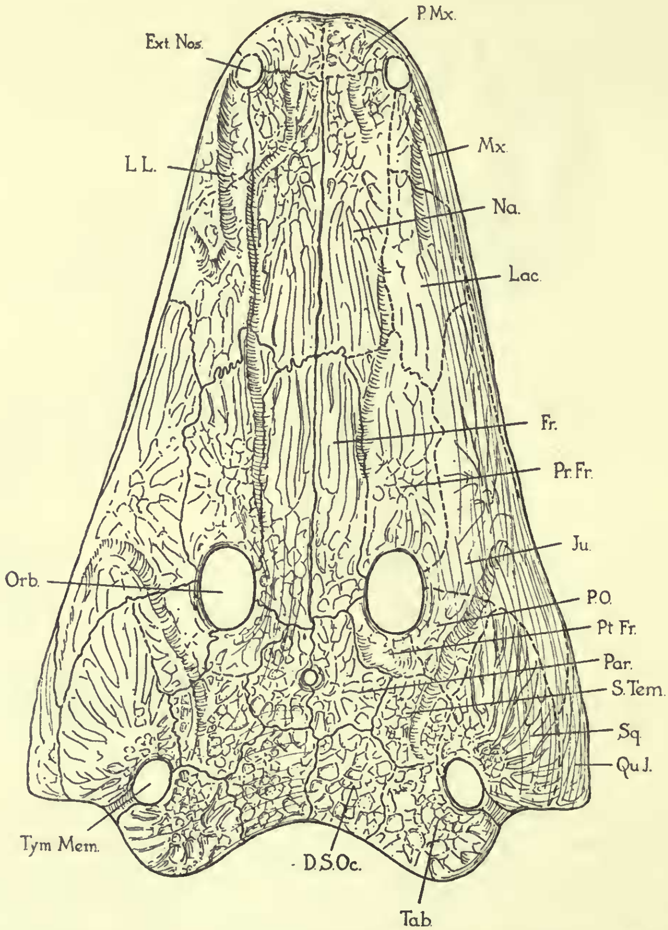

Fig. 5. *Paracyclotosaurus davidi.* The skull viewed from above, with its distortion corrected. × 1/6.

outward and upward over a rounded border above the pterygoid. Above this groove the bone extends upward until it ends, its admedian surface evidently embedded in a thick cartilaginous side wall of the braincase (between the proötic and the sphenethmoid). On the outer surface the bone has a deep notch separating the attachment to the pterygoid from the lower end of a special admedian process extending downward and a little forward laterally to the basisphenoid cartilage, and perhaps also to the parasphenoid. This notch must have been converted into a foramen by the parasphenoid or pterygoid, and no doubt transmitted a blood vessel.

The remainder of the skull consists of a series of membrane bones, attached to one another by interdigitating sutures which are not often seen. The whole outer surface is covered with bone except for orbits, nostrils, the pineal foramen, and the completely enclosed openings in which lay the tympanic membranes. The dermal bone coating the head is massive, about 2 cm. thick, and the individual bones of which it is composed were so tightly attached to one another by interlocking sutures that they withstood the blow from which the animal presumably died. In the cast actual

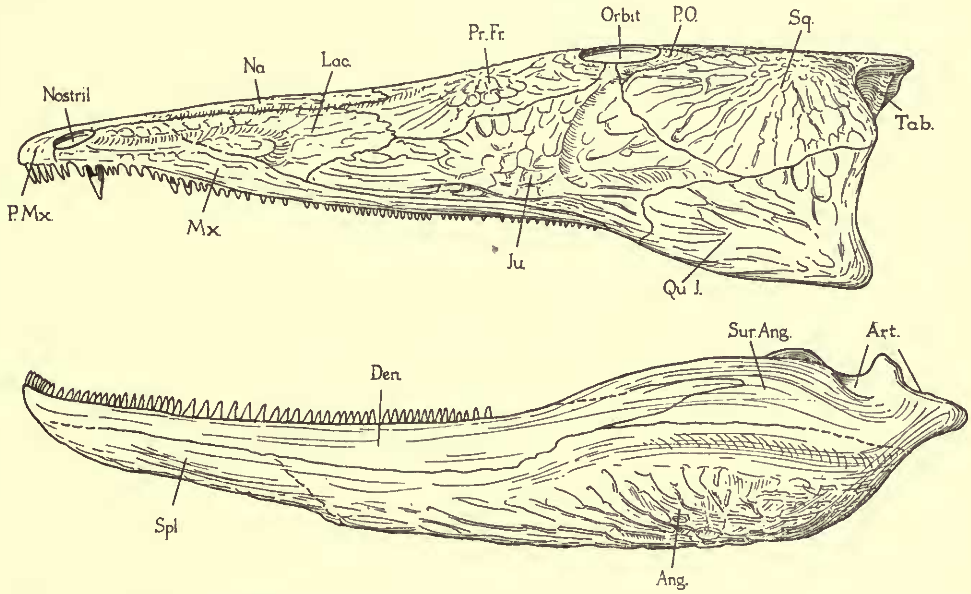

FIG. 6. *Paracyclotosaurus davidi*. Skull and lower jaw seen from the left. × 1/6.

sutures are seldom visible, but in most places the distribution of the pitted and grooved ornament determines their direction rather precisely. The general skull pattern differs very little from that found in other capitosaurs ; the only striking peculiarity is the closure of the otic notch by a fusion behind it of the outer end of the tabular with a special shelf passing backward from the hinder border of the squamosal in front. The tabular is an unusually large bone, forming a wide upper surface behind the tympanic space. It is nearly as long from back to front as the dermosupra-occipital.

Palate. The palate has the normal pattern of an advanced labyrinthodont. The quadrate condyles, though ventral to the occipital condyles, lie essentially in the same transverse plane, so that the quadrate ramus of the pterygoid is short and unusually laterally directed. The sub-temporal opening through which the jaw-closing muscles passed down to the lower jaw is large, but not unusually so ;

and the flange formed by the ectopterygoid and pterygoid, which in labyrinthodonts is usually applied to the inner surface of the lower jaw, is vestigial. It is impossible to determine the sutures between the pterygoid, ectopterygoid and palatine; but it is evident that the three bones form the outer border of the large palatal vacuity, their respective parts being indeterminable. The pterygoid is toothless. The palatine bears an alternative pair of large teeth, about 2·6 cm. high, immediately behind the internal nostrils, set as always in a common recess. A similar tooth seems to be shown on the vomer. Behind these "tusks" is a single series of teeth set close to the maxillary suture of the palatine and ectopterygoid bones, numbering in all 56 to 60. The series is essentially uniform, teeth being shed and replaced occasionally. An individual tooth is attached to the bone on the bottom of a very shallow depression. It is a triangular structure, flattened antero-posteriorly, attached to the bone by a base rather more than twice as wide across the jaw as it is long. The outer side is rounded and convex in profile, the inner a little concave, the point (where it might be expected to meet the teeth of the lower jaw) is also rounded and smooth. The tooth is as high as it is wide at its base, and separated from its neighbours by about its own thickness, the height being uniformly 9 or 10 mm. only. The elongated, narrow internal nostril, whose inner border is probably largely made by the vomer, is bordered by a row of similar but much smaller teeth which ends posteriorly at a short set of some six or seven very small conical teeth mesial of the first palatine tusk. The maxilla bears a close-set series of teeth, which decrease somewhat in size backwards. These teeth agree in structure with those of the palate, from which they are separated only by a very narrow wedge-shaped continuous groove. In all probability the series continued round the premaxilla.

The teeth of the lower jaws, carried entirely by the dentaries, are slightly enlarged copies of those in the upper jaws. They bite within the maxillary row and laterally to the palatal row.

The only large teeth—those on the palatines and vomers—are about an inch high, little higher than the marginal teeth, and were evidently unsuitable for the capture of any big animal, into whose body they could not penetrate far enough to kill. Further consideration of the animal's diet is left until after the description of the whole skeleton.

Lower jaw. The lower jaw is well preserved and has a normal labyrinthodont structure. The articular is fused with the surrounding bones, and is articulated with the quadrate, so that no complete description can be given. This articulation is extremely wide, fitting the quadrate condyle and rising mesially as a powerful process to articulate with the front face of the inner end of the quadrate condyle. The bone has an analogous process rising behind the outer condyle, to form the hinder border of a deep cylindroid notch, which assures accurate closure of the mouth. Behind this a massive conical retroarticular process projects directly backward for about 8 cm. behind the axis of the articulation. The surangular, fused with the articular, projects forward, bounding the 19 cm. long suprameckelian vacuity through which the masticatory muscles pass down into the hollow jaw. A prearticular bone, attached to the inner side of the articular, stretches forward parallel to the surangular forming the inner border of the muscle opening, which is closed at the front by the third coronoid, a narrow bone wedged in between the dentary and the prearticular. There is a series of apparently three coronoids attached to the inner surface of the dentary, widely exposed above the splenial and postsplenial bones. Their upper border may lie free above the shelf of the dentary to which they are attached ; none bears any teeth, though they bound and held in place the strip of gum from which dentary teeth arose.

Jaw musculature. The nature of the ornament on the outer surface of the lower jaw makes it certain that the masticatory muscles can have had only an infinitesimal, if any, attachment to the outer surface. The flat upper surface of the surangular, which stretches forward from immediately in front of the articular surface, seems unlikely to have given attachment to a muscle. Its character and width are similar throughout its length, and a muscle attached immediately in front of the condyle could have very little value. It probably represents the limit of the cheek, lateral to the masticatory muscles. These would arise from the skull roof and pterygoid, passing downward and inward, through the opening between the surangular and prearticular, to the cavity of the jaw, and probably extending forward past the large inner fenestra to an insertion on the inner surface. A muscle arising from the skull roof, at the attachment of the pterygoid to it, and passing down to the upper surface of the surangular at its mid-length, would be only some 10 cm. long, and perhaps placed about the same distance from the articulation ; a range of shortening by a quarter of its length would allow the mouth to open only about 15 cm. at the front of the jaw. An attachment to the point within the cavity of the jaw immediately below would double the depth of the opening, and an extension forward to the front of the internal mandibular vacuity might well double it again, the palate then being nearly at right angles to the jaw. The relative position of the occipital and quadrate condyles shows that if the lower jaw rested on the ground, as must often have been the case, it would be moved forward as the mouth was opened by raising the skull.

Vertebral column. The vertebral column is articulated from head to tail, and in general is undisplaced. In *Mastodonsaurus* (which is not remote from the Capitosaurs) the 1st vertebra is a continuous structure whose anterior face bears a pair of articular facets for the occipital condyles, below and between which a canal for the notochord opens. This passes obliquely through the bone, and opens behind, a little below the neural canal. There is a small fused neural arch, and no rib facet. No such structure can be found in this specimen. The blow which the body suffered on the left side of the head disarticulated that structure, so that the occipital condyle lies some 6 or 7 cm. to the right of the mid-line of the first two recognizable elements. Of these the anterior, which is perhaps the intercentrum of the 1st vertebra, differs from all others throughout the column. The rest are crescentic—half rings surrounding a large notochordal space—their upper ends narrowing and eventually becoming rounded. The 2nd intercentrum is peculiar only in that it is divided into right and left halves meeting below the notochord by extensive flat surfaces. The 1st intercentrum is also paired, and the left element (which alone is known) lies nearly in articulation with the corresponding bone of the 2nd, differing from this (like the corresponding bone of *Eryops*) by the absence of an upstanding process lateral to the notochord. Its anterior face does not show any definite cup for articulation with the rounded condyle. A left half of a neural arch, though found behind and above the left half of the 2nd intercentrum, probably belongs to the 3rd intercentrum, which has none associated with it. It corresponds generally with those found further back in the column, having similar cartilage-covered facets for articulation with pleurocentra, a short transverse process truncated by a rib facet, and a peculiarly small anterior zygapophysis with a rounded articular surface. Thus we have to find neural arches for vertebrae 1 and 2, and the right half of 3. Lying dorsal to and on the right of the two anterior intercentra are six strange bones, forming a dorsal series of two, a ventral of three, and still further down a fragment which may be a rib head. These bones should be determinable as the missing neural arches, but I am unable to identify them.

From this point backward the vertebral column is continuous, and the ribs attached to it are identifiable. There is a systematic change in structure from front to back. Such vertebrae as nos. 5, 6 and 13 (see Text-fig. 7) have a large semi-cylindrical intercentrum whose upper border has a semicircular notch for the notochord, on either side of which the bone was rounded and presumably capped with cartilage. In side view the bone is somewhat wedge-shaped, its mid-ventral border being widest, and the lateral surface is recessed between out-turned ridges. Toward the summit, near the hinder edge, is a large shallow concavity, offset from the outer surface, for the capitulum of the rib. The neural arch, apparently composed of paired elements in many parts of the column, has a short neural spine rising above the posterior zygapophyses and ending abruptly. Its anterior face turns forward to form anterior zygapophyses, below which lie the two sides of the neural canal, a relatively large cylindrical space. The lower surface of the neural arch is cut out to form the roof of the neural canal, on each side of which it bears a nearly rectangular facet for articulation with the cartilaginous pleurocentrum. Laterally to this facet lies a transverse process of varied length whose outer end is abruptly truncated by a rib facet.

Observation shows that mid-ventrally the intercentra met one another with a minimum of ligament between them, so that a measured length of 20·5 cm. is occupied by six intercentra—with individual lengths mid-ventrally of 3·4 cm., 2·9 cm. and 3·1 cm. in three directly measurable cases. The more anterior intercentra are massive structures nearly as high as they are wide, with a cylindroid ventral surface. No. 13 is perhaps the extreme of this condition ; its intercentrum is wide and high, 3·6 cm. in length, and remains massive almost up to the extreme dorsal points which carry the outwardly and backwardly directed shallowly concave articulations of the ribs. By no. 21 the intercentrum, still 3·5 cm. long, has become very shallow, about 3·6 cm. in contrast with 5·5 cm. in no. 13. No. 27 has an intercentrum 3·9 cm. long, 7 cm. in maximum width (compared with 9·2 cm. in no. 13). The intercentrum has a flatly cylindrical lower surface and almost straight, vertical, lateral surfaces, with large rib facets placed posteriorly and extending very nearly to its summit. The transverse process is short, extending only 2 or 3 mm. on the ventral surface beyond the intercentrum. No. 28, the sacral, does not show the intercentrum, but its neural arch differs in the depth and massiveness of its transverse process. In nos. 32 and 33 the neural arches are fused on the left side, all trace of zygapophyses having vanished, but on the right the neural spines are not continuous, and the anterior zygapophysis of no. 33 is well shown. The intercentra are very square cut, with an essentially flat ventral surface, and a large facet for the rib head filling the hinder part of the lateral surface. There is a very small, short, down-turned transverse process, and the rib is articulated by two heads. The positions of the completely cartilaginous pleurocentra are well shown.

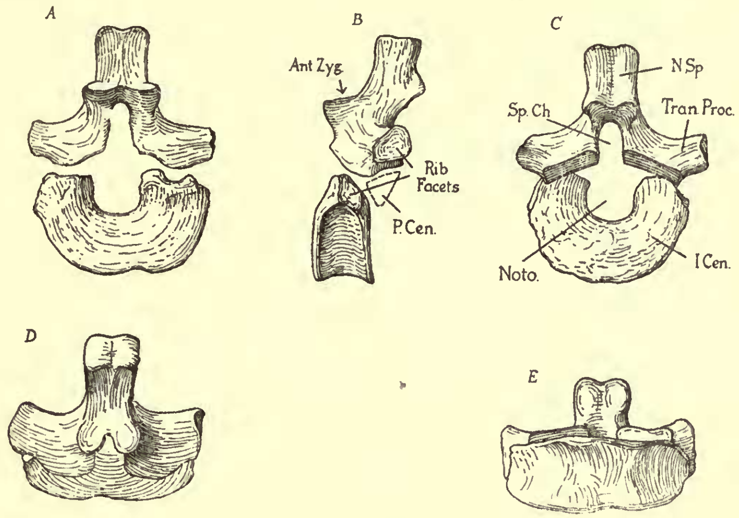

FIG. 7. *Paracyclotosaurus davidi.* Vertebra No. 13. A, from in front. B, left side. C, behind. D, from above. E, below. × 1/4.

These conditions continue down the tail, haemapophyses appearing at no. 36. Here the intercentrum is little more than a quadrangular sheet of bone, a little hollowed above, bearing a large downward and slightly backwardly directed chevron below and with a rib facet on the posterior end of its lateral border. The neural arch has a well-defined neural canal, lateral to which it extends out to a thickened and rounded end, which is presumably the upper part of the rib facet. Pre- and post-zygapophyses are well formed, with their articular faces at little more than right angles to one another.

Ribs. Ribs are in position from the first vertebra until they cease at the 36th. The first one is seen from below on the left side. It appears to be single headed, and is 7·6 cm. long. Proximally it is a thin, nearly vertical, bony sheet, but distally a peculiar ridge runs from its anterior surface making the bone about 2 cm. in maximum thickness. It extends outward practically horizontally. The upper end of the second rib is more than 3 cm. deep, and had a cartilaginous head which articulated with the appropriate facet on the intercentrum and the unknown neural arch. The bone is wide proximally, then becomes nearly circular in section, but widens distally, foreshadowing the conditions in those which follow. The ribs belonging to vertebrae 3, 4 and 5 are remarkable (cf. Pl. 29), for they are attached to the flat outer ends of the transverse processes, bone to bone, with little space remaining for cartilage between them. But the capitular part of the wide upper end of the rib fails to meet the facet on the intercentrum, to which it was attached in life, by about two centimetres, obviously a measure of the thickness of the cartilaginous capitulum. The rib then stretches out laterally and backward at about 45° to the mid-line. The ribs attached to vertebrae 3, 4, 5 and 6 are peculiar because their distal parts are widened so that they overlap one another and provide a large base of attachment to the muscles, the serrati anteriores, passing to the scapula. This widening is abrupt ; the slender shaft of the rib, distal to a dorsal ridge it bears, is roughly circular in section, and later rapidly widens to become at least 8 cm. across, the lower border being inturned as a flange. Ribs, 3, 4 and 5 thus combine to form a firm, powerful, flat surface some 8 × 20 cm. for the attachment of the scapula. From the seventh or eighth vertebra backward the ribs are

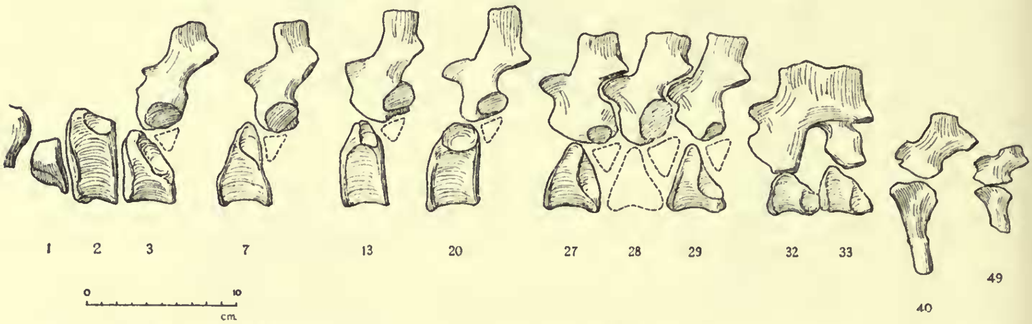

FIG. 8. *Paracyclotosaurus davidi*. Occipital condyle and selected vertebrae numbered below 1, 2, etc. No. 28 is the sacrum ; note large rib facet. Nos. 32 and 33 are abnormal in the continuity of their neural arches on this side. × 1/5.

essentially straight, simple, bony rods. Both sacral ribs are preserved, supplementing one another so that the complete structure is shown. The head, whose confluent faces carried a single cartilage cap which articulated with the transverse process and intercentrum of the sacral vertebra, is 6·2 cm. deep, with a maximum thickness of 2 cm., so that its attachment to the vertebral column is powerful. The bone rapidly narrows, and at 7 cm. from the attachment is only about 2 cm. thick. It then widens, its anterior surface being hollowed out so that it ends in two separated processes which must have met and been attached to the inner surface of the ilium a little below its upper border. The area of such contact is very small, the attachment being presumably reinforced by ligaments, as it presumably was in *Eryops* and certainly was in embolomerous amphibia. It seems clear that there is only a single sacral. The anterior caudal vertebrae still carry two-headed ribs.

The vertebral column is thus largely cartilaginous, but with well-formed zygapophyseal articulations and rib attachments. It was evidently capable of lateral movement though it is improbable that this would be through any extensive arc—except in the tail which curves round abruptly at nearly a right angle. Flexure in a dorso-ventral direction was probably very restricted.

Shoulder girdle. The primary shoulder girdle is most easily discussed after the membrane bones which carry it have been described. The interclavicle is a sheet of bone a little longer than wide ; the anterior end stretches forward as a narrow process and the middle strip may have been visible on the lower surface between the clavicles. The bone otherwise is rhomboidal with its three other corners rounded. Its visceral surface is shallowly concave a little in front of the mid-point, and quite posteriorly there is a small, shallow, but well-marked depression which is somewhat asymmetrical, opening backward to the left of the mid-line and presumably supporting the heart. The ventral surface is very largely covered by the usual pitted and

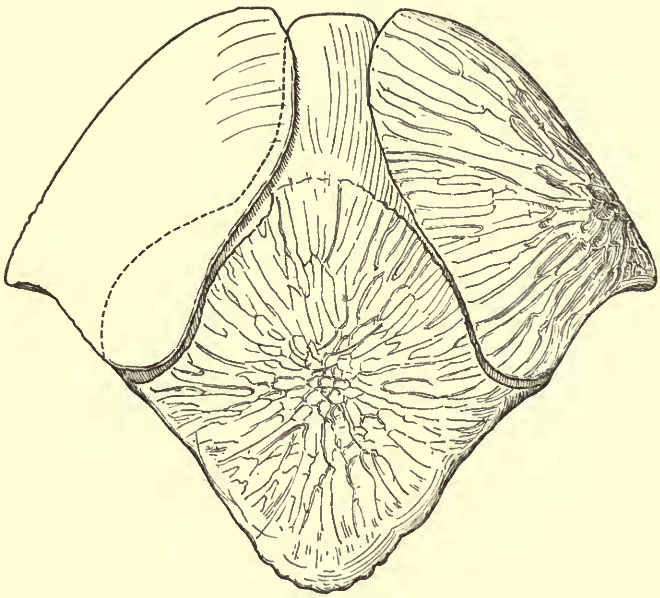

FIG. 9. *Paracyclotosaurus davidi.* Interclavicle and clavicles in articulation, from below. × 1/6.

ridged " ornament ", which extends to the borders of the bone in its posterior third, but ends abruptly laterally where the ventral surface has a sudden step dorsally for a centimetre or more, forming a recess into which the lower end of the clavicle fitted.

The clavicles are almost completely preserved and undistorted. They fit the recesses in the interclavicle sufficiently well to make the whole structure certain ; it is possible that they met anteriorly below the interclavicle.

The dorsal process of the clavicle is formed by an upturning of the lateral border of the bone, so that its outer surface lies at about 60° to the upper surface of the clavicle, or some 55° to the ground. This dorsal process is firmly attached to the ventral part of the bone by a base about 13 cm. long and (at its maximum) 3·5 cm. thick. The process is about 14 cm. high and 12 cm. antero-posteriorly ; its upper border slopes down a little in front, and the outer surface below it is excavated into a pocket, about 4 cm. deep, across its whole width, presumably for a musculus cleido-mastoideus. Below it the anterior part of the lateral surface is recessed on a definite oblique line.

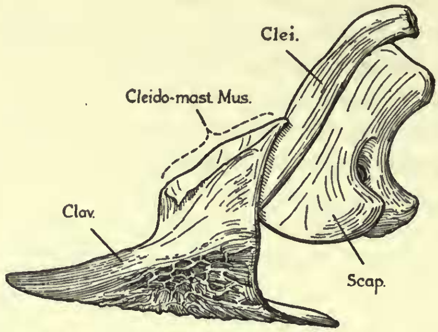

FIG. 10. *Paracyclotosaurus davidi.* Left clavicle in articulation with the cleithrum and scapula. × 1/6.

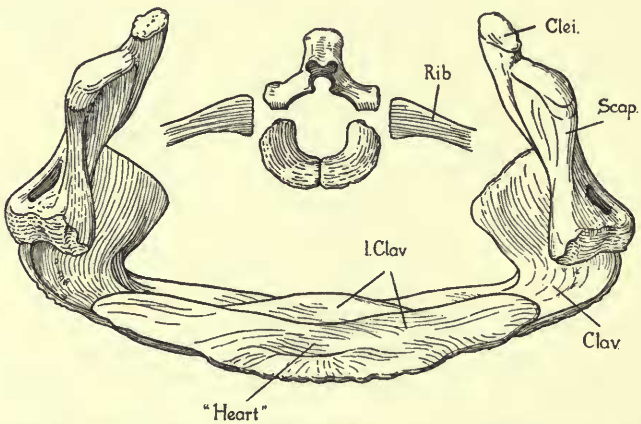

FIG. 11. *Paracyclotosaurus davidi.* The shoulder girdle in position with respect to the vertebral column and ribs, viewed from behind. × 1/6. (The intercentra and ribs belong to the second vertebra, the neural arch, to the third.) The figure shows the inclination of the dorsal processes of the clavicles towards one another as they pass forward and upward, so that the structure may lie between the hinder ends of the lower jaws. The modelling of the upper surface of the interclavicle to support the heart and other structures is shown.

The left cleithrum remains firmly attached to the scapula. It is a massive rod (4 cm. by 3 cm. in section at mid-height) which, beginning at a " blunt point " at the lower end of the scapula, rises to overhang the upper end of that bone by some 4 cm. The overhang slopes backward as a partial cap to a cartilage. The anterior face of the lowest 9 cm. of the bone is shallowly concave, and articulated with the hinder border of the dorsal process of the clavicle. Thus the position of the scapula is known with certainty, and that of the glenoid cavity can be inferred with accuracy.

The shoulder girdle thus built up is placed so far forward that the anterior parts of the clavicles and interclavicle lie directly below the braincase, the ascending ramus of the clavicle lying well within, but close up to, the hinder border of the cheek. The glenoid cavity for the humerus is about 18 cm. behind the quadrate.

The scapula is so small an ossification in the large cartilaginous scapulo-coracoid that nothing of the glenoid cavity is preserved, though the great thickening of the bone, below and behind, to more than 7 cm., shows its position. There is a large supraglenoid foramen passing forward and downward above the glenoid cavity. The position of the bones in the matrix, evidently still in articulation, gives a measure of the thickness of the cartilaginous caps to long bones, and to the glenoid cavity of the scapula ; it seems to be usually about one centimetre.

The humerus may be interpreted as a reduction of that of *Eryops*, differing in being much less completely ossified, in having the rugged muscle attachments of that animal reduced to very small proportions, and in presenting only the merest indication—by a small out-turning of the surface—of the huge hemispherical knob which in *Eryops* gave attachment to the radius. The limb has become a paddle, not a leg capable of supporting more than half the animal's weight in air. In fact all the limb bones of this animal greatly resemble those of *Trimerorhachis*.

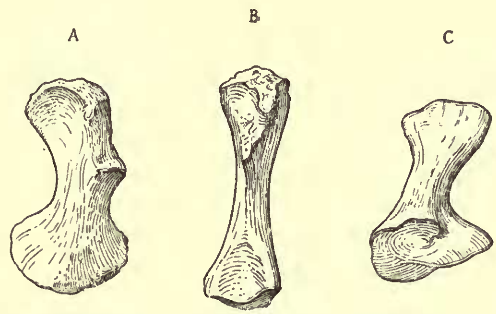

FIG. 12. *Paracyclotosaurus davidi*. A, the right humerus from below. B, the left femur from below. C, the left ilium, lateral aspect. All × 1/6.

The radius and ulna, about 8 cm. long, have widened extremities, once cartilage covered ; and the sum of their widths distally is about 8 cm., the presumed width of the entirely cartilaginous carpus, which is apparently about 5 cm. long and 8·5 cm. wide, judging from the widths of the heads of the five metacarpals. The middle metacarpal supports a finger with three phalanges whose total length is just under 8 cm. The first digit has a short, very massive, metacarpal which is followed by two phalanges, of which the second has a rounded and widened end, and a ligament attachment well marked on its palmar surface. The metacarpals do not overlap one another. The phalangeal formula is 2, 2, 3, 3, 2.

Pelvis. The pelvis is remarkable because it is much wider between the iliac crests than it is between the acetabula. The ischium was evidently narrow, though all its borders, except the lateral, were extended by cartilage. The pubis is largely represented by an impression through a layer of skin and is a relatively large sheet containing some ossification, the width across the pair much exceeding that across the ischia (Pl. 30). The wide expansion of the pubis, presenting the greatest possible contrast to that of *Eryops*, illustrates the general flattening and widening of the body found in the Triassic labyrinthodonts. It gives some indication that the tail was sharply marked off from the body by its much smaller width.

The femur is longer and thicker in the shaft than that of *Eryops* with which it was compared. The head bore a large cartilaginous cap; the lower end, abruptly truncated but continued in cartilage, seems to have carried two condylar knobs. The massive shaft has a low crest running along its lower surface, ending proximally at a ventral process, the homologue of the meeting point of the three great ridges of the femur of *Eryops*. This bears a series of well-marked muscle (or ligament)

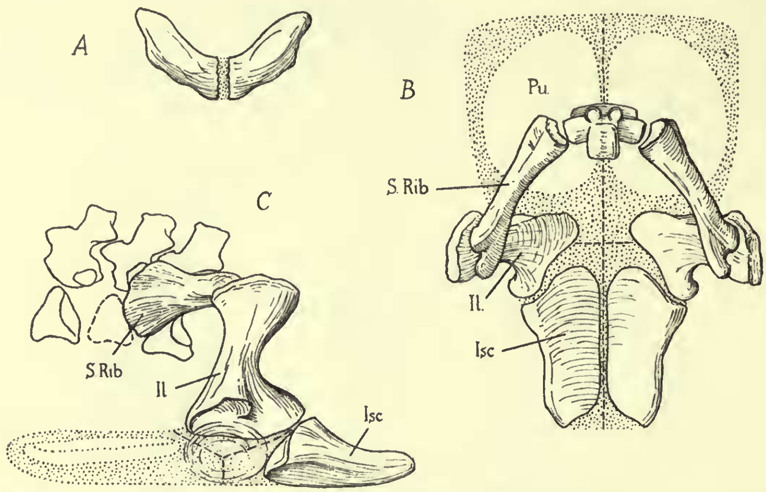

FIG. 13. *Paracyclotosaurus davidi*. Restoration of the pelvis. × 1/6. Cartilage is restored in the dotted areas, and the meeting of the three bones in the acetabulum is conventional. A, the ischia from in front; B, the pelvis from above. C, the pelvis from the left side.

insertions. The tibia, relatively massive, is incompletely known. No trace of the fibula is preserved. The tarsus is unossified, but there remain a series of rather scattered metatarsals and some phalanges. These merely show that the foot greatly resembled the hand in both size and structure.

Skin. The animal's skin is largely preserved as an impression, over part of the dorsal surface of the body, and of the ventral surface especially in the pelvic region. Block 14, dorsal surface (Pl. 31), lies from 15 to 30 cm. to the left of the mid-line opposite vertebrae 23–25. It bears an impression of the skin in an area where it has been rucked up in a manner which suggests that it was flexible, although it contained closely set, bony scales. These are irregularly oval in plan, ranging from 3·5 × 5 mm. to 9 × 6 mm. in size, devoid of definite ornament and set quite irregularly, but not in contact with one another. Their thickness cannot be measured, but appears to be less than 1 mm. They are calcareous, and presumably bony. An area of 50 square cm. contains more than one hundred scales.

A plastic cast of the ventral surface below the pelvis shows a clearly recognizable area of skin about 20 cm. square (cf. Pl. 30). Posteriorly a strip of skin with a torn anterior edge stretches across from the upper end of a femur on to a misplaced ischium. It then spans a gap until it is supported by another flat bone (presumably the other ischium), and then passes over another gap, where it is shown as an unsupported sheet some 3 mm. thick that continues over the ventral surface of a pubis, cracked by some accident with the cracks showing through the skin. It continues on to the other (misplaced) pubis. It is puckered in a convincing manner where the torn edge rests on the ischium. There is no suggestion that this ventral skin contains any bony scales, but it has a delicate surface sculpture of small pits which are clearly recognizable.

Such preservation of large areas and thicknesses of skin is remarkable, but it is paralleled by an ichthyosaur skull (No. R.509, D. M. S. W. Coll.) from the *planicostatus* zone between Lyme Regis and Charmouth. Here the skin is about 2 mm. thick, and in part it retains its cellular structure (Whitear, 1956).

III. BODY SHAPE AND MODE OF LIFE

The mode of life of the labyrinthodont described above should be discoverable, in part, from its unusually completely known structure. The small distortion of the head can easily be allowed for, and the complete preservation of skull and jaws makes its shape certain; its length is 60 cm. The right hinder corner of the head is essentially undistorted and shows that the skull at its point of greatest depth is almost exactly as high as the lower jaw. Similarly the lower jaw symphysis is the same height as the skull above it. Thus, at its point of greatest height, the head was essentially of oval section, 22 cm. high and 44 cm. wide. The nostril, orbit and tympanic membrane are all directed upward. Whether the eye could be projected upward above the head to give a horizontal view, as in the frog, is impossible to determine, but it may have been so.

The first rib is short, but the second, which is in undisturbed position, implies a body width of at least 35 cm., 10 cm. behind the condyles. The shoulder girdle is a rigid structure, the membrane bones lying in, or immediately below, the skin having a maximum width of 44 cm. at a point a little behind the lower jaws. The clavicles are upturned so that they incline inward, their minimum width of 23 cm. lying between the lower jaws, the interclavicle projecting along the throat below the skull for 15 cm. The maximum width of the body at the shoulder may well have been 53 cm. The forelegs, in a position of rest, would give a total width between the middle fingers of the forwardly directed hands of 87 cm. The distance of the sacral vertebra behind the skull is 115 cm. The body thus has a minimum height of 16 cm., and a width of more than 20 cm. The tail is about 50 cm. long, and is probably flattened laterally. The total length is approximately 225 cm.

The weight could be estimated by making a number of assumptions, but has little meaning in an aquatic animal. Roughly the creature is larger than a man in bulk and presumably in weight, but it may well have had no weight when submerged, depending on the size of the inflated lungs. On land it could no doubt walk to some extent, making a track little less than a yard wide, with a stride of perhaps 20 cm. As the individual prints of the well-preserved forefoot would be about 100 square centimetres, the track would consist of two strips of forefoot prints, with similar hindfoot tracks just within them, and with a wide streak of body impressions. In water it is probable that little but the ends of the fingers and toes would make impressions, the body streak probably not being seen It seems probable that the short tail could have had some use in swimming, though inadequate for rapid movement.

The animal's food may be considered here. It has a feeble dentition ; the only teeth which could be driven into the body of an animal seized in the mouth are those on the vomers and palatines, and these stand very little above the maxillary teeth, a close-set row lacking points of any kind. It is very likely that the creature caught its food as the living Giant Salamander is said to do—by waiting until the prey came near, then quickly opening its enormous mouth and swallowing it. The most probable food would be small fishes, up to some 15 cm. long, which swam in shoals. Fishes of such dimensions in the form of *Promecosomina*, a holostean, are those most abundantly found with the labyrinthodont.

How the animal breathed is uncertain. Had it done so as *Megalobatrachus* perhaps does, by moving the floor of the mouth by muscles attached to the hyoid and branchial arches, some of these elements would probably have been ossified, and none is. The ribs surround, at least, the upper part of the body, and articulate with the vertebral column by a wide and essentially two-headed upper end, attached obliquely to the column. They could presumably have been used in an essentially mammalian manner for breathing, though the rigidity of the shoulder girdle must have restricted rib movement there. But as the animal was probably as slow moving as a Giant Salamander, and the rate of its oxygen consumption very low, the buccal epithelium may have provided an efficient point of introduction of oxygen into the body, for the skin of the ventral surface is thick, and the skin as a whole was perhaps unlikely to be an important respiratory surface. It is difficult to imagine any such individual moving far, and impossible to imagine it traversing any very different environment.

IV. SYSTEMATIC POSITION

In 1914, when I first saw this animal as an impression, I referred it to the genus *Cyclotosaurus* on the grounds that its skull was in general structure like that of any capitosaur, and the otic notch closed by contact of the tabular and squamosal laterally. At that time the only known cyclotosaur was still the type species " *Mastodonsaurus robustus* ", given the new generic name *Cyclotosaurus* by E. Fraas in 1889 ; Smith Woodward's little English form (*C. stantonensis*) was at that time referred to *Capitosaurus*. Since then new discoveries have increased the number of species of *Cyclotosaurus* to ten[1], and added a new genus, *Rhadalognathus* Welles (1947), with a

[1] Two other "species" have been referred to this genus without reason.

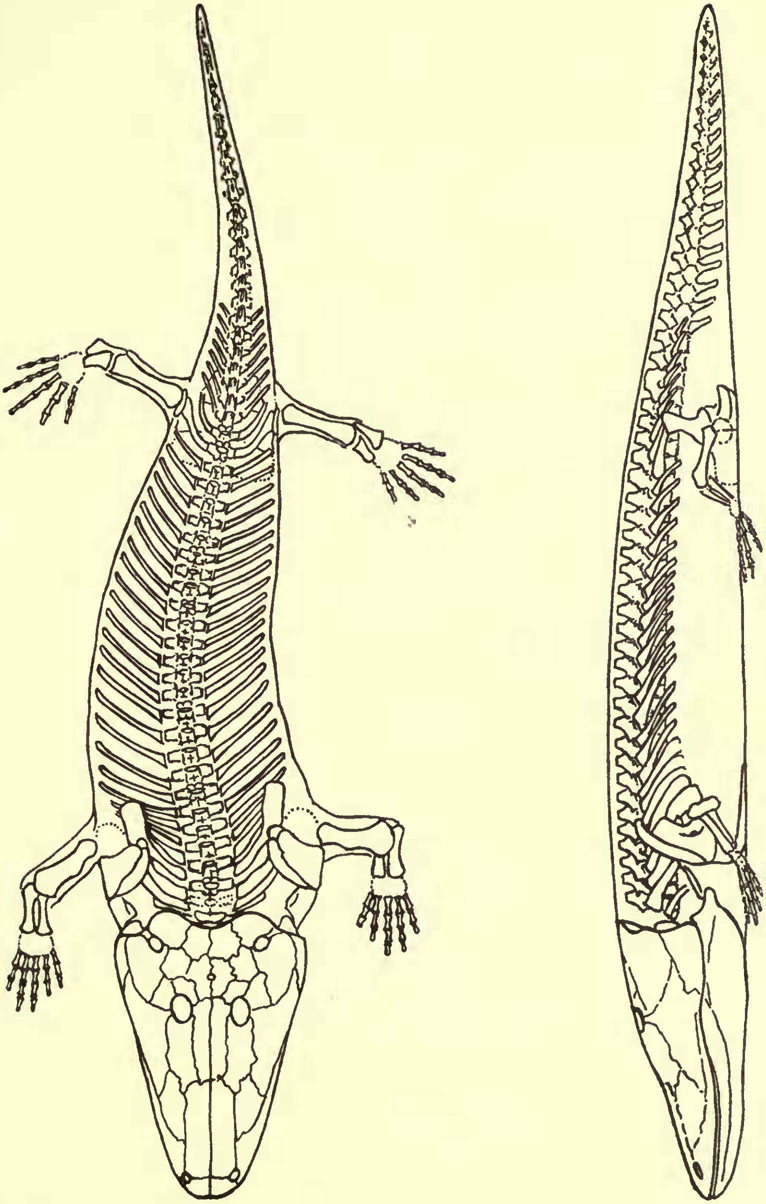

FIG. 14. *Paracyclotosaurus davidi.* Reconstruction of the skeleton in a walking pose. Total length approximately 225 cm.

similarly enclosed tympanic membrane. It is therefore necessary to examine each of these animals to distinguish which can rightly be referred to the genus.

The type species of *Cyclotosaurus*, *C. robustus* (Meyer & Plieninger) from the Schliffsandstein of the Lower Keuper, was described by Quenstedt (1850) and later by Fraas (1889). It is a large form with a triangular skull 53 cm. long in the mid-line with nearly straight sides except for the rounding off of the snout. The width posteriorly is about 43 cm. and the height at the occiput 5·1 cm. The skull is thus extremely flattened, though there is no reason to doubt that its real shape is preserved. Several skulls are known of similar proportions. There are large tusks on the vomers and palatines. The lower jaw has a maximum depth of 12 cm. at the articulation.

Cyclotosaurus posthumus Fraas (1913), from the Stubensandstein of the Upper Keuper, has a skull 53 cm. long and 42 cm. in maximum width, almost precisely the same as that of *C. robustus*. The height in the mid-line at the occiput is 6·3 cm. again similar to *C. robustus*, but the face is narrower, its lateral borders are concave, and the occiput lacks the deep concavity of the border found in *C. robustus*. There are large tusks on the vomers and palatines, and the dentition in general resembles that of *C. robustus*. It may well be placed in the same genus.

Cyclotosaurus mordax Fraas (1913), also from the Stubensandstein, was founded on a skull broken off about 2 cm. behind the orbits. The skull is flat and differs from *C. robustus* in having its interorbital width proportionally greater and its suborbital width less than in that form. It is also much shorter in relation to its width as judged from the palate. It differs from *C. posthumus* similarly, but may well be placed in the same genus.

Cyclotosaurus papilio Wepfer (1923), from the top of the Muschelkalk, is based on a fragmentary skull, clearly "*Cyclotosaurus*" by the complete enclosure of the tympanic membrane. The structural details are incomprehensible. It is thus not certainly determinable.

Cyclotosaurus ebrachensis Kuhn (1932), from the Middle Keuper of Oberfranken, was described from a complete skull about half the size of *C. robustus*. The general outline resembles that of *C. robustus*, but the orbits and tympanic membranes are relatively more widely set, no doubt a scale effect. The greatest width is 23 cm. and the height 3·2 cm., relatively more than in *C. robustus* and less than in *C. mordax*. It is evidently a member of the genus *Cyclotosaurus*.

Cyclotosaurus hemprichi Kuhn (1942), from the Upper Keuper (?Rhaetic) of Halberstadt, is an admirably preserved but, in part, scattered skull, excellently described. The skull is approximately 62·5 cm. long, 46 cm. wide, and the height (dorsal surface to quadrate condyle) is 11·4 cm. The depth of the occiput distinguishes this skull from all those listed above, and cannot be explained by growth, for it is little greater in size than the type species.

Cyclotosaurus stantonensis (A. S. Woodward) (1904), from Stanton, Staffordshire. Skull length 20·5 cm., width 15·3 cm., maximum height 4·2 cm. The depth of the occiput as a fraction of skull width agrees with *C. hemprichi* and differs from that of the type species. The skull is remarkable because the sutural connection of the exoccipital and pterygoid is short, whilst the quadrate ramus of the pterygoid has a well-developed post-tympanic flange, known in "*Capitosaurus*" (= *Parotosaurus*) but not in any other "*Cyclotosaurus*" (cf. Sushkin, 1927 : 273, 285).

"*Cyclotosaurus randalli*" Welles (1947), from the Moenkopi formation of Arizona, is founded on fragments including one showing a "closed otic notch" and part of a basis cranii. This species differs greatly, in the relations of the exoccipital, parasphenoid and pterygoid to one another, from any of the forms listed above and is evidently not closely related to them.

Rhadalognathus boweni Welles (1947) is founded on a very slender labyrinthodont lower jaw, impossible of comparison with those of capitosaurs. It is held by Welles, on the basis of associated fragments, to have had a closed otic notch. As reconstructed by Welles, the skull is unlike that of any of the cyclotosaurs mentioned above.

"*Cyclotosaurus spitzbergensis*" Wiman (1915) is an indeterminable fragment.

"*Labyrinthodon pachygnathus*" Owen (1842, pl. 46, figs. 6, 7) was recognized by Welles as being an English *Cyclotosaurus*.

Comparison of general proportions shows that the skull of the St. Peter's labyrinthodont differs from *C. robustus* (the type species of the genus), *C. posthumus*, *C. ebrachensis* and, presumably, *C. mordax*, in being much deeper in proportion to its length and width. In this matter it agrees closely with *C. hemprichi* and *C. stantonensis*.

C. stantonensis differs very greatly in the persistence in it of the post-tympanic flange of the pterygoid found in "*Capitosaurus*" (= *Parotosaurus*) and in the proportions of the tympanic cavity so far as it can be inferred. It retains more of the structure and proportions of this region in *Parotosaurus*, and appears to be a "primitive" form, not necessarily closely related to other cyclotosaurs and I therefore establish for it a new genus, ***Procyclotosaurus***.

C. hemprichi, however, very much resembles the Australian animal. It differs in the shape of the tympanic membrane, which is "triangular" in contrast to circular. But in the structure of the occiput (apart from the presence of a well-marked shelf on the exoccipital for the supraoccipital cartilage) the two are very alike ; the relation of the exoccipital to the pterygoid (Kuhn, 1942, pl. 1, fig. 1*b*), the structures shown in his pl. 1, fig. 3, and the structure of the quadrate-pterygoid region (pl. 3, fig. 1*b*) are extremely similar in the two animals.

The resemblances and differences set out above imply that the "*Cyclotosaur*" condition of total enclosure of the otic membrane by contact of the tabular and squamosal lateral to it has arisen more than once, and hence cannot by itself characterize a genus.

Thus *Cyclotosaurus*, founded on *C. robustus*, may include *C. posthumus* Fraas, *C. mordax* Fraas and *C. ebrachensis* Kuhn.

The species with deep skulls—the Australian skeleton which is the subject of this paper, and *C. hemprichi*—differ noticeably from the true cyclotosaurs. That these differences are significant is shown by the remarkable fact that their peculiarities occur in three magnificent skulls from the Middle Trias of East Africa in Mr. Parrington's collection (Field no. 48, Mkongoleko, Stockley's B.9. "Upper Bone Bed" (2 specimens) ; Field No. 135, Gingama, Stockley's B.26. "Upper Bone Bed") which might well be their ancestors, but not the ancestors of the typical flat-headed *Cyclotosaurus*. There are accordingly two distinct lines.

Thus the St. Peter's labyrinthodont is made the type of a new genus and species, ***Paracyclotosaurus davidi***, and with it is placed *C. hemprichi* of the extreme Upper Keuper of North Germany.

That the St. Peter's labyrinthodont and *Paracyclotosaurus hemprichi* belong to the same genus and one manifestly distinct, by its ancestry, from true *Cyclotosaurus* is of stratigraphical significance, for *P. hemprichi* comes from the " oberen Knollen Mergel " at Halberstadt, at the extreme top of the Trias, or perhaps even in the Rhaetic. Nothing in the structure of the St. Peter's animal is inconsistent with such a late age, but nevertheless it might be somewhat older, that is, earlier in the Upper Trias.

V. DESCRIPTION OF *SUBCYCLOTOSAURUS BROOKVALENSIS* gen. et sp. nov.

Parrington's East African animals, in so far as the dorsal surface of their skull is concerned, resemble a small " Parotosaur " skull from the Brookvale clays of the Hawkesbury Sandstone, shown in Text-fig. 15. This specimen is the mould of a skull broken so that the right border is lost, and very slightly distorted by pressure so that the orbits are no longer quite symmetrical. The proportions of the skull resemble those of most others of *Parotosaurus* and *Cyclotosaurus*, the preorbital length being 66% of the total mid-line length, the extremes amongst parotosaurs being 61% in the small *Cyclotosaurus ebrachensis*, and 71% in *Parotosaurus helgolandicus*. The skull is characterized by the small tabular without any trace of a " horn ", but with a round lappet that approaches the squamosal flange lateral to the tympanic membrane, failing to meet it by about its own width. The occiput between the otic notches is proportionately wide, a reflection of the small size of the skull. The skull is otherwise of normal *Parotosaurus* structure, but has a small internasal vacuity between the dorsal processes of the premaxillae. Lateral lines are often shown as continuous grooves with well-defined borders. A deep groove on the maxilla begins immediately behind and lateral to the nostril and passes straight back to the lachrymal, on which bone it turns outward and forward and ends abruptly. Another groove appears to begin on the maxilla, immediately lateral to that described above. It passes back just above the insertion of the teeth for the full length of the bone. The supraorbital groove begins abruptly on the dorsal surface of the premaxilla, immediately passes on to the nasal, and extends back on that bone close to its suture with the lachrymal, it then comes on to the prefrontal, passing on to the frontal where that bone enters the orbital border. Then as a well-defined groove it surrounds the hinder part of the orbit, turns vertically on to the jugal, and then backward to cross the point where jugal, quadratojugal and squamosal meet, continuing over the squamosal to pass back on to the body. There is a canal, really a series of pits, crossing the supratemporal. For this skull, whose characters are shown in the figure, I propose the new genus ***Subcyclotosaurus*** and the trivial name ***brookvalensis***.

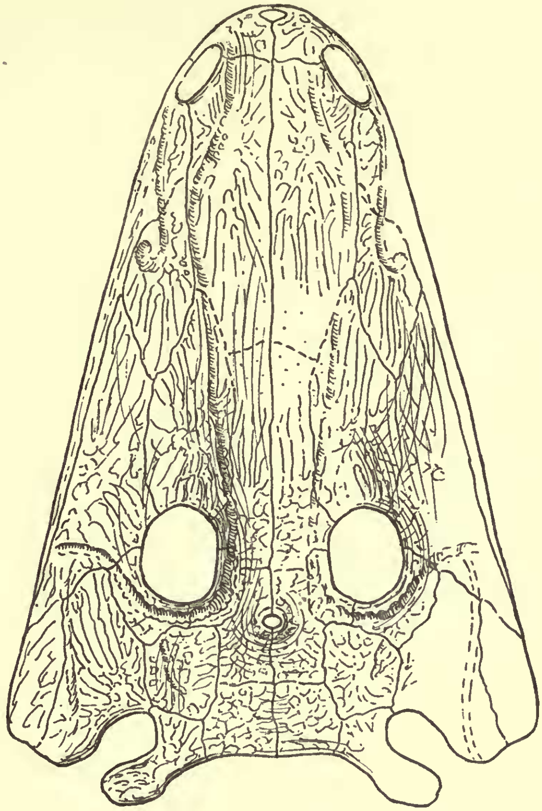

FIG. 15. The skull of *Subcyclotosaurus brookvalensis* gen. et sp. nov. × 3/4. The missing narrow strip on the right is restored from the left side, and the distortion corrected. The short tabular processes approaching but not meeting the squamosal are characteristic. [R. T. Wade Coll., Australian Museum, Sydney].

VI. ASSOCIATED BRACHYOPID

Some time after the discovery of *Paracyclotosaurus* Mr. Dunstan found another large piece of ironstone in the St. Peter's quarries which retained impressions of characteristic labyrinthodont bones. A flexible cast from this mould shows part of the dorsal surface of a skull, sometimes from both surfaces, and the upper surface of an incompletely preserved left pterygoid. So far as the material goes it is excellently preserved, but as the skull was partly disarticulated before burial, the bones displaced, and only the hinder part—not including an orbit—available, it is difficult to determine its systematic position with any assurance.

Text-fig. 16 represents the bones of the upper surface of the head as they lie, with the upper surface of the pterygoid. The mesial part of the skull table was clearly flat, but toward the outer end of the dermosupraoccipital it turns a little downward, so extending to the end of the tabular. The hinder border is there carried by the squamosal, continuing in the same direction until it rather suddenly turns vertically and descends, presumably to meet a quadratojugal. The well-preserved left dermosupraoccipital has a thickness of nearly 2 cm. on its hinder surface, which continues on to the tabular, where it is no longer seen. The tabular, shorter from back to front than the dermosupraoccipital, is wide, ending in a point laterally, presumably housed in a small groove in the hinder border of the squamosal, which continues laterally to it, so that there can be no trace of an otic notch. The supratemporal, which is cracked across and the two parts separated by about a centimetre, is completely shown as a relatively large bone surrounded by the dermosupraoccipital, tabular, squamosal, postorbital and presumably also by the missing postfrontal. The bone is crossed obliquely by an unusually wide and deep lateral line groove, which ends abruptly before reaching the parietal border of the bone. The post-orbital, lying lateral to the supratemporal and attached to it by visible suture,

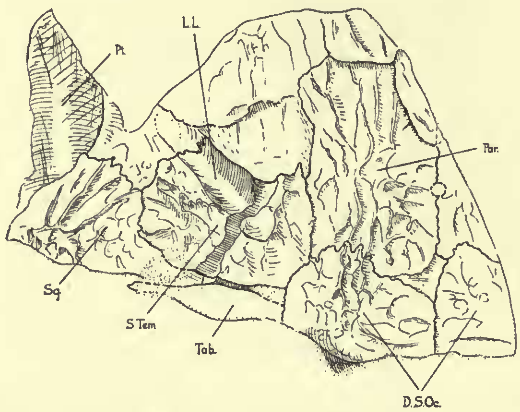

FIG. 16. Fragment of associated Brachyopid skull, drawn from a plastic cast from a block of ironstone from the Wianamatta Shales of St. Peters. × 1/3.

bears a continuation of the wide lateral line groove, and has long sutures with the supratemporal and squamosal, and with what is presumably the jugal. The squamosal is firmly attached by suture to the jugal, postorbital and supratemporal, its lateral border for the quadratojugal implying an unusual mode of attachment. No recognizable piece of the orbital margin remains, but immediately in front and on the left side of the parietal is a wide spread of scarcely ornamented bone, which toward the middle line is attached to a small area of well-ornamented bone, probably a frontal: these are obviously misplaced with respect to the rest of the skull.

There can be no doubt that this skull belonged to a Brachyopid, but it is scarcely determinable generically, and is left unnamed.

VII. ACKNOWLEDGMENTS

The foregoing paper is a long delayed fulfilment of a promise made very many years ago to Sir T. W. Edgeworth David. The development of the specimen, so skilfully carried out by the late Mr. F. O. Barlow, required many years of patient work using the laborious methods then available, and the intervention of two wars much increased the delay in finishing the task of preparation.

I can only express my gratitude to these two men, and to the original discoverer Mr. B. Dunstan. I also owe thanks to Professor Medawar for the hospitality of the Zoology Department of University College, London, and to the Royal Society for enabling Miss J. Townend, who is responsible for all drawings which illustrate the paper, to work with me, and also to Mr. W. Brackenbury for the photographs on Pls. 29–31.

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VIII. KEY TO ABBREVIATIONS IN TEXT-FIGURES

Ang., angular.
Ant. Zyg., anterior zygapophysis.
Art., articular.

B. Pt., space formerly occupied by the cartilaginous basipterygoid process.
Bd. Ves., foramen for a blood vessel.

Clav., clavicle.
Clei., cleithrum.
Cleido-mast. Mus., cleido-mastoid muscle insertion.

D. S. Oc., dermosupraoccipital.
Den., dentary.

E. Pt., epiterygoid.
Ec. Pt., ectopterygoid.
Ept. Bas. Art., facet on epiterygoid which articulates with the basis cranii.
Ex. Oc., exoccipital.
Ex. Oc. Cav., cavity in the exoccipital.
Ext. Nos., external nostril.

Fem., femur.
Fr., frontal.

Gass. Gang., groove in the epipterygoid for the Gasserian ganglion.

I. Cen., intercentrum.
I. Clav., interclavicle.
Il., ilium.
Int. Nos., internal nostril.
Isc., ischium.

Ju., jugal.

L. L., lateral line groove.
Lac., lachrymal.

Mx., maxilla.

N. Sp., neural spine.
Na., nasal.
Noto., space for notochord.

Orb., orbit.

P. Cen., pleurocentrum.
P. Mx., premaxilla.
P.O., postorbital.
Pal., palatine.
Par., parietal.
Par. Sp., parasphenoid.
Pin. For., pineal foramen.
Pr. Fr., prefrontal.
Pr. Ot., proötic.
Pt., pterygoid.
Pt. Fr., postfrontal.
Pu., pubis.

Qu., quadrate.
Qu. J., quadratojugal.

S. Rib., sacral rib.
S. Tem., supratemporal.
Scap., scapula.
Sp. Ch., spinal chord.
Sph. Eth., sphenethmoid.
Spl., splenial.
Sq., squamosal.
St., stapes.
Sur. Ang., surangular.

Tab., tabular.
Tran. Proc., transverse process.
Tym. Cav., tympanic cavity.
Tym. Mem., tympanic membrane.

Vo., vomer.
II, notch in sphenethmoid probably for optic nerve.
V^1, ophthalmic branch of N. trigeminus.
V^2 & ^{3}, maxillary and mandibular branches of N. trigeminus.
XII, foramen for nerve XII.